13. Reliability of cranial morphology in reconstructing Neanderthal phylogeny

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Abstract

The usefulness of cranial morphology in reconstructing the phylogeny of closely related taxa is often questioned due to the possibility of convergence or parallelism and epigenetic response to the environment. However, it has been suggested that different cranial regions preserve phylogenetic information differentially. Some parts of the face and neurocranium are thought to be relatively developmentally flexible, and therefore to be subject to the epigenetic influence of the environment. Other parts are thought to be particularly responsive to selection for adaptation to local climate. The basicranium, on the other hand, and in particular the temporal bone, is thought to be largely genetically determined and has been argued to preserve a strong phylogenetic signal with little possibility of homoplasy. Here we test the hypotheses that cranial morphology is related to population history among recent humans, and that different cranial regions reflect population history and local climate differentially. Morphological distances among ten recent human populations were calculated from the face, vault and temporal bone using three-dimensional geometric morphometrics methods. The distance matrices obtained were then compared to neutral genetic distances and to climatic differences among the same or closely matched groups. Results indicated a stronger relationship of the shape of the vault and the temporal bone with neutral genetic distances, and a stronger association of facial shape with climate. Vault and temporal bone centroid sizes were associated with climate and particularly temperature; facial centroid size was associated with genetic distances. Temporal bone shape was more successful in tracking older population history than vault shape. Of the three cranial regions, it is therefore most appropriate for phylogenetic reconstructions among fossil humans. Analysis of temporal bone shape of both recent and Middle-Late Pleistocene humans showed Neanderthals to be morphologically very distant from both recent and fossil modern humans, indicating that Neanderthals represent a distinct evolutionary lineage.

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Introduction

Among the major problems in phylogenetic reconstruction from skeletal morphology is the potential unreliability of morphological characters in reflecting phylogeny (among species) and population history (within species). Convergence, parallelism, reversals and epigenetic changes are often thought to overwhelmingly influence craniofacial anatomy and to erase any phylogenetic information it might have contained (see e.g., Lieberman et al., 1996; McCollum, 1999). This criticism has been leveled most recently by Collard and Wood (2000, 2001), who found that diverse cranio-dental datasets failed to reproduce molecular phylogenies in hominoids and papionins. These authors concluded that cranial morphology cannot be used to successfully reconstruct primate and human phylogenetic relationships.

This view, however, is not universally accepted, and some researchers have proposed a differential preservation of phylogenetic information in different cranial anatomical regions. Olson (1981) suggested that the basicranium is the most genetically determined and evolutionarily conservative aspect of the cranium, and as such should be highly phylogenetically informative. This view was echoed by Wood and Lieberman (2001), who also proposed that different cranial regions reflect phylogenetic information differentially. Since the basicranium develops from cartilaginous, rather than intramembranous, origin, they suggested that its development is genetically determined, so the resulting adult morphology is only minimally influenced by environmental factors. On this basis they argued that the basicranium is more phylogenetically informative and more appropriate for phylogenetic reconstruction than the facial or cranial vault regions, which are thought to be more developmentally plastic. Recent analyses of the complex three-dimensional shape of the petrous portion of the temporal bone have provided tentative support for these hypotheses. Using three-dimensional geometric morphometrics, Harvati (2001) found that temporal bone shape tracks relationships among recent human populations better than the occipital and parietal regions of the skull. Lockwood et al. (2004) also analyzed three-dimensional temporal bone landmark coordinates to reconstruct the hominoid phylogeny, with results that closely matched the molecularly derived relationships.

Even if a cranial region reliably reflects underlying genetic variation, it will not be useful for phylogenetic reconstruction if it is particularly responsive to selection for adaptation to climate, other aspects of the local environment or behaviors. The face, in particular, has previously been linked to climatic adaptation (e.g., Coon et al., 1950; Roseman and Weaver, 2004) and to dietary and masticatory practices (e.g., Hylander, 1977; Rak, 1986; Smith, 1983), probably through a combination of epigenetic responses and genetic adaptation. The shape of the vault has also been linked to climatic adaptation (e.g., Beals, 1983; Roseman, 2004).

Here we tested the reliability of morphological evidence from three regions of the cranium – face, temporal bone and vault – in tracking population history by comparing morphological distances among recent human groups to those derived from a large number of microsatellites (neutral genetic loci, Rosenberg et al., 2002, see below). Ten globally distributed recent human groups represented in the genetic database (or their close neighbors) were also represented in our three-dimensional cranio-facial landmark database (two African, two Asian, two European, two Australasian, one Middle Eastern and one New World Arctic, see Table 1). Mahalanobis squared distance matrices (hereafter Mahalanobis D^2), corrected for unequal sample sizes, were calculated among the recent human groups based on landmark coordinates from each of the three cranial regions. The